

APPENDIX 3: EFFECTIVE POPULATION SIZE AND RECOVERY PLANNING

(References included in the Literature Cited section of the plan.)

Effective population size provides a standardized measure of the amount of genetic variation that is likely to be transmitted between generations within a population. Effective population size is a theoretical concept that allows one to predict potential future losses of genetic variation within a population due to small population size and genetic drift. Individuals within populations with very small effective population sizes are also subject to *inbreeding depression* because most individuals within small populations share one or more immediate ancestors (parents, grandparents, etc.) after only a few generations and will be closely related.

A number of factors affect the effective population size of a species. For example, unequal sex ratios can significantly affect effective population size because male and female adults of the parent generation must each contribute 50 percent of the genes to the progeny generation regardless of their relative numbers. Hence, effective population size will be lower than the summed census number of both sexes, and will also be less than four times as large as the number of adults of the less common sex. For example, a population derived from one male and three females would have an effective population size of three; a population derived from one male and an infinite number of females would have an effective population size of four (Crow and Kimura 1970). The latter population would experience the same amount of genetic drift as a population derived from only 2 males and 2 females. Similarly, populations with high fluctuations in abundance over time (or generations) will have an effective population size that is approximated by the harmonic mean of the effective population sizes of each generation. This harmonic mean will be influenced significantly by the generation with the lowest effective population size because that generation represents the “bottleneck” through which all genetic variation in future generations must pass.

It is relatively easy to relate effective population size to theoretical losses of genetic variation in future generations and, thus, provide conservation guidelines for effective population size. Based on standardized theoretical equations (Crow and Kimura 1970), the following guidelines have been established for maintaining minimum effective population sizes for conservation purposes:

- Effective Population Size > 50 to prevent inbreeding depression and a potential decrease in viability or reproductive fitness of a population (Franklin 1980);
- Effective Population Size > 500 to minimize loss of genetic variation due to genetic drift and maintain constant genetic variance within a population resulting from a balance between loss of variance due to genetic drift and an

increase in variance due to new mutations or gene migration (Franklin 1980; Soule 1980; Lande 1988);

- Effective Population Size $> 5,000$ to maintain constant variance for quasi-neutral, genetic variation that can serve as a reservoir for future adaptations in response to natural selection and changing environmental conditions (Lande 1995). The rationale here is that the effective population size needs to be large enough to minimize genetic drift and the potential loss of genetic material that may confer a slight, selective advantage under existing or future environmental conditions.

In contrast to establishing conservation guidelines for effective population size, it is much more difficult to quantitatively relate the breeding structure of a species and census numbers of populations to effective population size so that the 50/500/5000 guidelines can be applied at the appropriate scale. The longevity, life histories, and structure of individual breeding units (*i.e.*, *local populations*) must be understood sufficiently to relate the number of observed adults within a particular population (and in a particular generation) to a genetic *effective number of breeders*. Conceptually, this latter quantity will be similar to effective population size in the classical, textbook sense. Second, it is necessary to understand the amount of gene flow among geographically adjacent breeding units (*e.g.*, bull trout reproducing in adjacent tributaries to a river) so that, over multiple-generation time-scales, effective breeding numbers at the local population level can be considered part of a larger *metapopulation* with respect to applying the 50/500/5000 guidelines. For example, very small amounts of gene flow may not be sufficient to increase the effective number of breeders within a given local population above effective population equal to 50. However, in a combination of such populations that experience gene flow between them, effective breeding numbers for the metapopulation may be greater than 500. In this latter situation, one would predict significant genetic variation among breeding units and comparatively small amounts of genetic variation within individual breeding units, but the combination (or metapopulation) as a whole could potentially retain significant amounts of genetic variation over time. The key to understanding the evolutionary and conservation implications of such a breeding structure is knowing whether the individual breeding units, or local populations, are completely isolated reproductively or whether some gene flow does indeed occur, thus allowing genetic material to be reintroduced if lost from a particular population.

The effective population size $> 5,000$ rule derived by Lande (1995) relates largely to future evolutionary potential. Hence, the scale for its application are expected, in most cases, to be much larger than the spatial and temporal scales at which one applies the “50/500” rules. For example, the effective population size > 50 and effective population size > 500 guidelines may be most applicable on time scales

encompassing 1-5 and 5-50 generations, respectively: at least two generations are necessary to produce “inbred” individuals after a population has gone through a major population bottleneck (*i.e.*, effective population size < 50), and a substantially greater number of generations are usually necessary for genetic drift to be significant (*i.e.*, when effective population size < 500). On the other hand, the effective population size $> 5,000$ guideline relates to the evolutionary persistence of a species over some defined geographic area such that, if extinction does occur, recolonization from elsewhere is precluded geographically or is unlikely to occur over microevolutionary time scales (*e.g.*, 50 or more generations).

The effective population size > 5000 guideline would apply to a population unit that is significant from an evolutionary perspective. This population unit could range from a local population to multiple recovery units and theoretically should represent a distinct population segment. Based on the best genetic information available at the time of listing (1998), the U.S. Fish and Wildlife Service identified both the Columbia and Klamath rivers as distinct population segments (63 FR 31647). Additional genetic information since the time of listing indicates that subdivision of the current Columbia River distinct population segment into smaller units may be warranted. A research need has been identified to evaluate whether the Columbia River distinct population segment can be further divided. The bull trout recovery plan has identified the collection of genetic information and the potential re-classification of the Columbia River distinct population segment as a research need. Division of any additional distinct population segments will follow existing policy, and will consider both the discreteness, and significance of the proposed unit (61 FR 4722).

Rieman and Allendorf (2001) have performed computer simulations of bull trout populations to understand the relationship between the observed number of adults, or spawners, within a local population and effective population size. Their best estimate of effective population size is 0.5 to 1.0 times the mean number of adult fish spawning annually. This translates into maintaining between 50 and 100 spawners per year to minimize potential inbreeding effects within local populations. The spatial scale for such a local population would encompass all adult fish with approximately equal probability of interbreeding amongst themselves within a single year or generation. One would expect such a population to include very few immigrants from another population or breeding unit. Between 500 and 1,000 spawners per year would be needed to maintain genetic variation and minimize the deleterious effects of drift. The appropriate spatial for maintaining genetic variation for bull trout would be most frequently applied at the core area level.